NOTHING IN TAXONOMY MAKES SENSE EXCEPT IN THE LIGHT OF EVOLUTION: EXAMPLES FROM THE CLASSIFICATION OF *RANUNCULUS*[1]

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ABSTRACT

Biological classification aims at establishing ordering systems for organisms. Principles of classification, however, differ in their criteria and in their information content. Cladistic classification emphasizes information on descent, but the strict application of logical inclusiveness leads in practice to disregard of modification and to a lack of information on evolutionarily relevant features. Phenetics provides information on similarity regardless of descent. Evolutionary classification maximizes information on evolution by combining information on descent and modification, but it relaxes the requirement of inclusiveness. In practice, this means accepting holo- and paraphyletic taxa, but rejecting polyphyletic groups. Review of a recently published case study of the species-rich and cosmopolitan genus *Ranunculus* demonstrates how evolutionary classification can be performed in practice. A hypothesis of descent was reconstructed by phylogenetic analysis of DNA sequence markers plus morphological and karyological characters. Based on this backbone phylogeny, information content on morphology, karyology, and ecology was used as a criterion for delimitation of infrageneric taxa. This concept resulted in the subdivision of a more basal, paraphyletic *Ranunculus* subg. *Auricomus* and the holophyletic *Ranunculus* subg. *Ranunculus*. On a sectional level, 14 holophyletic and two paraphyletic sections plus one monotypic section were classified. Holophyletic sections mostly reflect extinction gaps, while paraphyletic groups appear in clades that have reticulate evolution and/or ecological shifts. Classification of paraphyletic and monotypic sections preserves information on morphology, ecology, and evolutionary processes. This pluralistic approach is justified as it best reflects the diversity of the genus. The principle of broadening criteria maximizes information on descent and modification. Evolutionary classification facilitates practicability and stability of taxonomic work, as the broadening of criteria restricts the number of equally valid options for classification. For users, preserving information content on phenotypes aids practicability, because the connection to traditional literature and to modern information systems is optimally maintained.

Key words: Classification, evolution, holophyly, paraphyly, phylogeny, practicability, Ranunculaceae, *Ranunculus*.

The title of this article on the classification of *Ranunculus* is inspired by Dobzhansky's (1973) famous statement that "Nothing in biology makes sense except in the light of evolution." This article discusses the importance of incorporating information on evolution into biological classification. Much has been disputed before on theory, and the issue of paraphyly has remained controversial (Ashlock, 1971; Duncan, 1980; Stuessy, 1987, 1997; Brummitt, 2002; Mayr & Bock, 2002; Ebach & Williams, 2004; Hörandl, 2007; Hörandl & Stuessy, 2010; Schmidt-Lebuhn, 2012, Stuessy & Hörandl, 2014). The current practice of classification, however, does not reflect the variety of opinions. Above the species level, most taxonomists adhere to principles of cladistic classification. In this article, I first briefly review the relationship of evolution, phylogeny, taxonomy, and their functions as information systems. The presentation of *Ranunculus* as a case study will hopefully reveal practicable solutions for evolutionary classification. Finally, I discuss some general points regarding contemporary taxonomy.

Evolution means "change," and therefore is a process. In the broadest sense, it is a process of populations undergoing descent with modification over generations. Contemporary taxonomy takes evolution partly into account as almost all modern authors agree that biological classification above the species level should reflect descent (e.g., Mishler, 2009; Hörandl & Stuessy, 2010). Descent is best reflected by the DNA molecules carrying heritable information from one generation to the next, and DNA sequence data have become the marker of choice for phylogenetic reconstruction of descent. Descent,

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however, also establishes patterns of similarity in descendants because of the shared inheritance of features. Modification, in contrast, is the raw material of variation and for selection to act upon, and therefore the base of change and diversification. Modification, however, exists at different levels of organismic organization—at the level of micro- or macromolecules, genes, chromosomes, enzymes, membranes, cells, organs, organisms, or behavior. These processes are not necessarily reflected in the currently used DNA sequence markers. In flowering plants, modification can have its background in gene expression patterns and epimutation, chromosomal change, gene duplication, or even whole genome duplication, and such modifications may have fundamental effects on phenotypes (e.g., Cubas et al., 1999; Soltis et al., 2009; Chanderbali et al., 2010). Moreover, population structure, community structure, and even ecological interaction do have effects on the phenotype via selection and even direct influence on epigenetic control mechanisms in complex feedback loops (e.g., Bossdorf et al., 2008). Therefore, modification cannot be so easily pinpointed to a certain type of data, and modification has often been neglected in phylogenetic systematics in theory and practice (see examples in other papers of this symposium). Modern cladistic classification regards only a minimum of information on modification, i.e., that of a synapomorphy, which is in practice restricted to DNA sequence data (the problem of a loss of information on character combinations has been discussed elsewhere; Hörandl, 2010).

Taxonomy aims at establishing ordering and information systems on organisms (Stuessy, 2009). In general, ordering systems are based on defined and well-circumscribed entities with information content, i.e., on classes. In biological classification, organisms are sorted into taxa according to certain criteria, with the aim that the taxon, as a class, has theoretical foundation, information content, and predictivity. The criteria for grouping determines the information content of a taxon (Fig. 1):

- Cladistics bears information on descent and accepts monophyletic (inclusive) groups only (better termed as holophyletic; see Hörandl & Stuessy, 2010, on terminology). In asymmetrically bifurcating or reticulate phylogenies, divergence via autapomorphies or reticulate evolution cannot be recognized (Hörandl, 2006). This concept bears the danger of loss of information on the modifications of the phenotype (Fig. 1B).
- Phenetics bears information on modification only, as modification (as a process) results in dissimilarity (as a pattern); inclusiveness according to the criterion of similarity is usually handled in a relaxed fashion according to practicability. Phylogenetic status is not relevant. Therefore, holo-, para-, and polyphyletic groups can be accepted. This concept suffers from lack of information on descent and from various competing options for grouping (Fig. 1C).
- Evolutionary classification bears information on descent plus modification and partly inclusiveness. It accepts holophyletic and paraphyletic groups, as paraphyletic groups do share ancestry, but are just not strictly inclusive. The concept also effectively reduces options for grouping (Fig. 1D).

For cladistic classification, information content on modification other than synapomorphies is simply not relevant. The information content of autapomorphy, symplesiomorphy, and conflicting characters is not being recognized. Instead, the focus on descent has driven taxonomists to a purely logical criterion, i.e., that of inclusiveness, which means that all descendants must be included. Inclusiveness is not necessarily a biological feature, but a construct of human thinking. From an evolutionary point of view, strict inclusiveness can never be achieved in biological systems, because this criterion would require a completely static system; evolution, however, is change, and change always means that transitions happen from one class to the next. Inclusiveness is needed for maximum predictivity of a group. However, it should be emphasized that most classes outside biology are not strictly inclusive, but do have fuzzy borders: colors, languages, species, community structures, religions, cultures—all these commonly used classes are not strictly inclusive, but nevertheless have predictivity (Holynski, 2011). No human language is logical and inclusive, but nevertheless works for carrying information. Also, for phenetics, inclusiveness has less priority, because similarity as the main criterion also often has fuzzy borders. Information content of a class, however, is not given by inclusiveness per se, but by the choice of criteria. To maximize information content on evolution, therefore, it is more important to broaden criteria (descent and modification) than to put emphasis on strict inclusiveness. Therefore, inclusiveness is not a primary criterion for evolutionary classification.

Evolutionary classification uses descent as a primary criterion to establish a backbone, and modification as a secondary one to make decisions for grouping (Fig. 1D). The priority is justified as shared ancestry usually causes similarities in the bauplan, simply because of shared inherited features, and this kind of similarity is usually informative about evolution. This method differs fundamentally

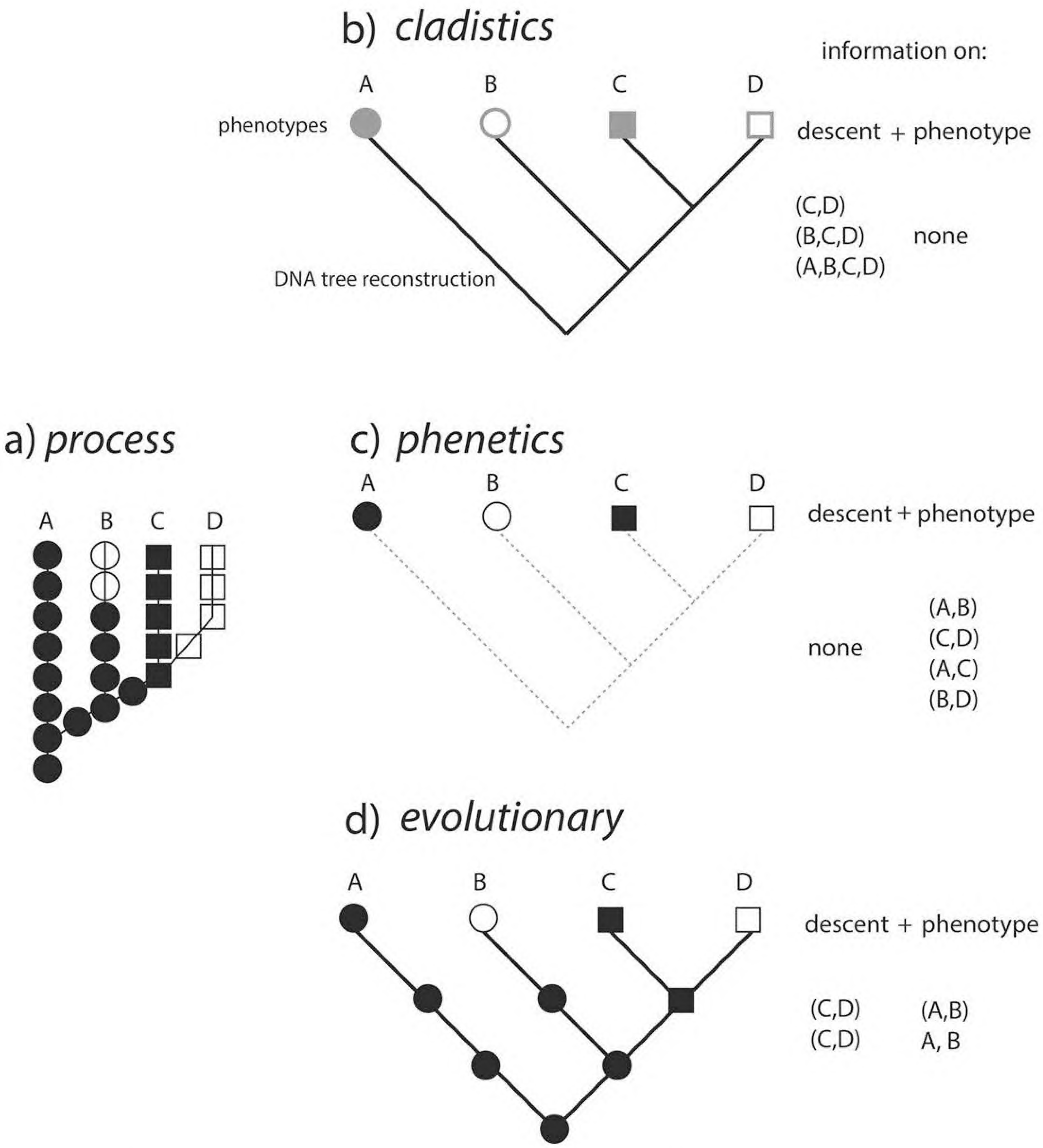

Figure 1. Scheme of information content of different classification concepts, with two characters each with two states mapped onto a phylogeny of four taxa (outgroup not shown). —A. Evolutionary process resulting in paraphyly (budding), with a phenotypic character evolving along lineages. B, C. Mapping of the character on a DNA sequence phylogeny and inferred grouping concepts. —B. Cladistics classification based on shared ancestry provides no information on phenotypic change and has three grouping options. —C. Phenetics based on the four symbols provides no information on descent and has four grouping options. —D. Evolutionary classification regards the phylogeny plus similarity and thus provides information on descent and modification; just two options for grouping are left.

from phenetics where similarity is the primary criterion, while descent was rather deduced from it in an interpretative, but not decisive fashion. Similarity as the primary criterion often has resulted in polyphyletic taxa in the past (for instance, plants with catkin-like inflorescences being classified as Amentiferae, which includes several, unrelated orders of angiosperms). Unfortunately, polyphyly and paraphyly have often been confused, and this confusion has been seen as a major argument against evolutionary classification. The problem arises from the inclusiveness principle of cladistics, as paraphyly and polyphyly apply to both non-inclusive groups, but otherwise rely on a fundamentally different *biological* criterion. A paraphyletic group is based on descent, it was once holophyletic, it once had a shared common ancestor, and shared features (symplesiomorphies) are a result of this shared ancestry (i.e., a former synapomorphy); see Hörandl and Stuessy (2010). The paraphyletic group appears in tree topologies usually as a basal grade with one or more holophyletic derivatives descended from it. Paraphyletic and holophyletic taxa are thus "convex" in the sense of Duncan (1980), whereby a subset of evolutionary entities is convex "if the path of line segments between any two members of the subset does not include phyletic line segments that are part of a path connecting two evolutionary units of a different subset."

A polyphyletic group, in contrast, never had a holophyletic stage in its evolutionary history. It is not convex sensu Duncan (1980). Its shared features (homoplasies) are not a product of descent. Homoplasy might have different genetic backgrounds; in angiosperms, the overall capacity of rapid shifting between morphological character states is quite well documented, and often just due to changed expression patterns of the same genes (e.g., Chanderbali et al., 2010). Reconstructions of ancestral states using morphological data alone are complicated, but that can be done on DNA backbone trees (e.g., Endress & Doyle, 2009). The members of a polyphyletic group would appear separated by several nodes in a molecular tree topology. (Perhaps it might be better to apply the term "aphyletic" to such groups as, in fact, there is no genealogy in terms of descent involved.) The term "polyphyletic" may be better applied to cases of multiple hybrid origins of a taxon, or segregation of characters in hybrid progenies; such cases also may produce a scattered distribution of character states onto a tree, but these patterns do have a genealogical background.

Classification of the genus *Ranunculus* exemplifies how evolutionary classification can maximize the information content of taxa. The genus is highly diverse and widespread, comprising about 600 herbaceous species (plus ca. 600 agamospecies), with a cosmopolitan distribution (Tamura, 1995; Hörandl et al., 2005; Emadzade et al., 2010). Variation and diversity exist at many different organizational levels. The present state of research has been summarized by Hörandl and Emadzade (2012): DNA sequence data (*matk/trnk*, *psbJ–petA*, and nrITS) are available for ca. 300 species, i.e., about half the genus. Chromosome counts and ploidy information are available for about one third of the species, while the great variation of the karyotype within the genus has been studied in detail for about 100 species (Goepfert, 1974; D'Ovidio & Marchi, 1990; Dahlgren, 1991; Baltisberger, 1994; Takahashi, 2003; Baltisberger & Widmer, 2009). Polyploidy occurs in ca. 40% of species and plays a major role in the diversification of the genus (Hörandl et al., 2005; Hoffmann et al., 2010; Hörandl & Emadzade, 2012). The morphological phenotype has been described for ca. 600 species; morphological data compiled with a stringent and comparable methodology for phylogenetic analysis have been compiled for ca. 200 species (Hörandl & Emadzade, 2012). Geographical distribution and related ecology are more or less known for all described species (summaries in Tamura, 1995; Hörandl & Emadzade, 2012). Ecological diversity is in general extraordinarily high, with species occurring both in freshwater and terrestrial habitats, ranging from semi-deserts to temperate forests and grassland, arctic-alpine tundra, from montane rainforests to anthropogenic habitats (Tamura, 1995). Because of its cosmopolitan distribution, the genus is represented in most regional and local bioinformation systems (floras, databases, and checklists) of the world.

The evolutionary history of the genus is fairly diverse. Recent biogeographical studies have demonstrated that long-distance dispersal and multiple colonizations of continents have shaped the evolutionary history of the genus (Emadzade & Hörandl, 2011; Emadzade et al., 2011). *Ranunculus* originated about 21 million years ago (Ma) and has a crown group age of ca. 18 million years (My); the genus diversified later on during the Cenozoic in several waves via various evolutionary processes. Many high mountain clades originated and diversified during the Quaternary (Emadzade & Hörandl, 2011) under the influence of Pleistocene glaciations. Hybridization occurs in many extant groups with or without polyploidy (Cook, 1966; Huber, 1988; Lockhart et al., 2001; Hörandl et al., 2005, 2009). Reticulate evolution may have also happened frequently in the evolutionary history of the genus, as it can be hypothesized from incongruent placements of some major subclades (e.g., *Ranunculus* sect. *Thora*) within the phylogeny in nuclear and plastid datasets (e.g., Paun et al., 2005).

Classification of *Ranunculus* should provide information on various evolutionary processes and organismic levels that have shaped the diversity of the genus. Neither morphology alone, nor a DNA-based phylogeny alone, could provide this information. Previous similarity-based infrageneric classifications of *Ranunculus* were always controversial, and traditional sections by Tamura (1995) appeared to be scattered over molecular trees (Hörandl et al., 2005). The infrageneric taxa show a mosaic-like pattern of character combinations, mostly without unique features, which has led to various taxonomic concepts, depending on the emphasis on selected characters (Hörandl & Emadzade, 2012). On the other hand, using information only on descent would make a classification of *Ranunculus* quite meaningless, as evolution acts in various ways, and modification plays a major role in diversification. Information is needed on karyology, phenotype, character evolution, and ecology to reflect the diversity of the genus. An infrageneric classification of subgenera and sections tries to meet these demands (Hörandl & Emadzade, 2012). Here I summarize the evolutionary history and features of accepted sections (Table 1) and review the new classification also with respect to different historical, theoretical, and practical aspects. A main goal of my discussion is to demonstrate the superiority of a pluralistic approach for classification over a strictly dogmatic theoretical principle. From this aspect, paraphyletic taxa are, in terms of information content, acceptable for classification if they bear information on structure, function, evolution, and ecology (see Hörandl & Stuessy, 2010).

EVOLUTIONARY HISTORY AND INFRAGENERIC TAXA OF *RANUNCULUS*

Ranunculus s. str. (sensu Emadzade et al., 2010) has been confirmed as holophyletic in all previous phylogenetic studies based on DNA data (Hoot, 1994; Johansson, 1995, 1998; Ro et al., 1997; Hörandl et al., 2005; Paun et al., 2005; Lehnebach et al., 2007; Gehrke & Linder, 2009; Emadzade et al., 2010; Hoffmann et al., 2010). The circumscription of the genus has recently been settled based on molecular and morphological data (Emadzade et al., 2010). This classification avoided a polyphyletic genus *Ranunculus* as it has been revealed by the molecular phylogenetic study by Hoot et al. (2008), which had focused on the position of *Hamadryas*. The only solution of a holophyletic genus *Ranunculus* sensu Hoot et al. (2008) would have been to merge all genera of the tribe into one genus. Such an extreme lumping would not reflect the diversity of the tribe and is not accepted by Eurasian and South American authors who emphasize morphological diversity on the generic level (e.g., Lehnebach et al., 2007; Wang et al., 2009). The classification by Emadzade et al. (2010) is to date the only solution of a holophyletic genus *Ranunculus*. Previous classifications based on morphology only rendered *Ranunculus* as polyphyletic (e.g., Tamura, 1995; Whittemore, 1997). The infrageneric classification by Hörandl and Emadzade (2012) was based on a phylogenetic backbone and a minimum of shared morphological characters of each group. We subdivided the genus into a paraphyletic *Ranunculus* subg. *Auricomus* and a monophyletic *Ranunculus* subg. *Ranunculus*, and we discriminated 17 sections, 14 of them being holophyletic, two paraphyletic, and one monotypic; we did not accept any of the previous polyphyletic sections. The acceptance of paraphyletic groups and one monotypic section was mostly justified by morphological and ecological information content.

HOLOPHYLETIC SECTIONS: EXTINCTION GAPS

Holophyly is a stage of evolution when the paraphyletic stem group, from which the ancestor arose, has gone extinct. Holophyletic groups, therefore, reflect historical extinction gaps (Hörandl & Stuessy, 2010). Most holophyletic groups can be related to biogeographical scenarios with massive extinction due to climatic changes. Nine of the 14 clades classified as sections occur predominantly in high mountain systems of the temperate to arctic zones and comprise mostly high alpine species (sections *Thora*, *Aconitifolii*, *Ranuncella*, *Epirotes*, *Leucoranunculus*, *Auricomus*, *Pseudadonis*, *Oreophili*, *Euromontani*; see Hörandl & Emadzade, 2011). Our dating analysis suggests that the origin of all these clades predates the Pleistocene (Emadzade & Hörandl, 2011). Glaciations and climatic cooling during the Pleistocene likely contributed to the extinction of paraphyletic stem groups, while later diversification and speciation happened mostly among cold-adapted taxa of alpine zones. Sections *Aconitifolii* and *Ranuncella* also include species from lower altitudes of the same geographical region (Paun et al., 2005). A global comparison of alpine taxa revealed that species from different mountain systems are related to species of adjacent lowlands rather than to species of mountain systems in other areas, which suggests that alpine groups have arisen independently several times from lowland ancestors (Hörandl & Emadzade, 2011). In previously glaciated areas, some holophyletic groups comprise only alpine species (sections *Epirotes*, *Leucoranunculus*, *Pseudadonis*); their lowland ancestors might have gone extinct (Paun et al., 2005; Hörandl & Emadzade, 2011). The shift to higher altitudes and ecological adaptation to alpine conditions may have established reproductive isolation among the ancestors of these clades in early stages of their evolutionary history, while geographical isolation and vicariant speciation were main drivers of speciation within clades.

Ranunculus sect. *Flammula* represents a holophyletic group with a strong ecological preference for wetlands and water habitats at lower altitudes. As all clade members share this ecology, it can be

Table 1. Survey of the accepted sections of *Ranunculus* (after Hörandl & Emadzade, 2012) and hypotheses on their evolution.

Nr.	Name	Phylogenetic status	Evolutionary origin	Main internal diversification processes	Key references
1	sect. *Thora*	holophyletic	ancient hybrid origin, Pleistocene extinction gap of stem group	allopatry	1, 2, 3, 4
2	sect. *Aconitifolii*	holophyletic	uncertain	adaptive radiation, also polyploidy	1, 2, 3, 4, 5
3	sect. *Ranuncella*	holophyletic	geographical and ecological isolation (orophytic)	radiation on Iberian Peninsula	1, 2, 3, 4, 5
4	sect. *Epirotes*	holophyletic	geographical isolation (orophytic)	ongoing speciation/gene flow	1, 2, 3, 4, 5
5	sect. *Leucoranunculus*	holophyletic	geographical and ecological isolation (orophytic)	allopatry, vicariant speciation	1, 2, 3, 4, 5
6	sect. *Pseudadonis*	holophyletic	early geographical isolation on New Zealand (orophytic)	hybridization, polyploidy, adaptive radiation	1, 2, 3, 6
7	sect. *Batrachium*	holophyletic	hybrid origin out of wetland group	ongoing hybridization, polyploidy, adaptive radiation	1, 2, 3, 7
8	sect. *Hecatonia*	paraphyletic	widespread stem group of former section	geographical isolation	1, 2, 3
9	sect. *Auricomus*	holophyletic	ancient extinction gap	hybridization, polyploidy, apomixis	1, 2, 3, 8
10	sect. *Flammula*	holophyletic	ancient extinction gap	long-distance dispersal, peripatry	1, 2, 3
11	sect. *Ranunculus*	holophyletic	dysploidy event	long-distance dispersal, geographical isolation, polyploidy	1, 2, 3, 9, 11
12	sect. *Polyanthemos*	holophyletic	ancient extinction gap	long-distance dispersal, geographical isolation, polyploidy	1, 2, 3, 11
13	sect. *Echinella*	monotypic	anagenetic, character evolution	—	1, 2, 10, 11
14	sect. *Trisecti*	holophyletic	uncertain; geographical isolation	no information	1, 2, 11
15	sect. *Oreophili*	holophyletic	geographical isolation (orophytic)	geographical isolation	1, 2, 3, 10, 11
16	sect. *Euromontani*	holophyletic	geographical and ecological isolation (orophytic)	adaptive radiation, also polyploidy	1, 2, 3, 10, 11
17	sect. *Ranunculastrum*	paraphyletic	Tethyan stem group of 16; geographical and ecological isolation (partly orophytic)	geographical isolation, ecological shifts	1, 2, 3, 10, 11

[1] Hörandl and Emadzade (2012).
[2] Emadzade et al. (2010).
[3] Hörandl et al. (2005).
[4] Hörandl and Emadzade (2011).
[5] Huber (1988).
[6] Lockhart et al. (2001).
[7] Cook (1966).
[8] Hörandl et al. (2009).
[9] Goepfert (1974).
[10] Paun et al. (2005).
[11] Emadzade et al. (2011).

hypothesized that the most recent common ancestor was a hydrophilous plant. The strong ecological specialization may have eliminated a less specialized and less competitive paraphyletic stem group. This clade combines conserved morphological features from *Ranunculus* subg. *Auricomus* (swollen achenes) and *Ranunculus* subg. *Ranunculus* (foveolate microstructure of achene surface); see Hörandl and Emadzade (2012, supplement 5). Whether this combination is adaptive or due to reticulate evolution requires further study.

Chromosomal change is another putative explanation for holophyly. In section *Ranunculus*, the origin of the clade can be related to karyotype evolution and a dysploidy event with a shift to a chromosome base number from $x = 8$ to $x = 7$. *Ranunculus* sect. *Polyanthemos*, a highly diverse and widespread clade of lowland to mid-altitude species, is sitting on a relative short branch and is also morphologically not strongly differentiated from its sister clade (Hörandl & Emadzade, 2012). *Ranunculus* sect. *Trisecti* from the Caucasus-Irano Turanian region is not well known; further studies are needed to understand its evolutionary history.

PARAPHYLETIC SECTIONS AND THEIR HOLOPHYLETIC DERIVATIVES

Two paraphyletic ecological groups were accepted by Hörandl and Emadzade (2012): *Ranunculus* sect. *Hecatonia* and *Ranunculus* sect. *Ranunculastrum*. They have different evolutionary histories. In both cases Hörandl and Emadzade (2012) could demonstrate that information content of paraphyletic taxa on morphology, ecology, and evolutionary process exceeds that of alternative cladistic classifications.

Ranunculus sect. *Hecatonia* forms a grade at the base of *Ranunculus* sect. *Batrachium* (Fig. 2); the relationship of some species to New Zealand alpine species (*Ranunculus* sect. *Pseudadonis*) may point at an older biogeographical connection via Antarctica. In all three sections, polyploidy is frequent and reticulate evolution has been documented (Fig. 3). However, so far we cannot see a clear progenitor-derivative relationship of certain diploid and polyploid taxa, but rather a wide-meshed network with one well-supported genetic cluster, *Ranunculus* sect. *Batrachium*, emerging out of it (see above). Polyploidy and multiple copies of the ITS of the nuclear ribosomal DNA are probably responsible for numerous conflicts between gene trees from different loci (Hörandl et al., 2005). *Ranunculus* sect. *Batrachium* is holophyletic in the total evidence approach, but not according to molecular data alone (Emadzade et al., 2011). Reticulate evolution, especially allopolyploidy, is probably the reason for equivocal results on shared ancestry. Neighbor-net analysis based on genetic distances (molecular combined dataset from Hörandl & Emadzade [2012]) indicates that several splits contribute to phylogenetic incompatibilities (see scale bar in Fig. 3). However, clustering of species of *Ranunculus* sect. *Batrachium* (Fig. 3) shows the genetic similarity within *Ranunculus* sect. *Batrachium*. The group might well have originated from an ancient hybridization event, but recent hybridization with members of other related sections has never been reported. The constancy of shared features (white flowers without a starch layer, U-shaped to ringlike to pyriform nectaries, wrinkles on the achene surface) speaks against a hypothesis of segregation of patterns in a hybrid swarm, but rather suggests a shared acquisition of these features together with the specialization to the aquatic habitat. Other characters, like creeping or floating habit, heterophylly, and the formation of dissected leaves in some taxa, are likely adaptive to the aquatic habitat, and show plasticity according to environmental conditions (Cook, 1966).

The problem is that recognizing *Ranunculus* sect. *Batrachium* leaves a paraphyletic group, *Ranunculus* sect. *Hecatonia*. Species of *Ranunculus* sect. *Hecatonia* differ from *Ranunculus* sect. *Batrachium* by mostly yellow petals with a starch layer and a smooth achene surface (except for *R. sceleratus*, with sometimes weakly wrinkled achenes). They colonize a broad range of habitats from wet soil in bogs and along ponds to semiaquatic habitats; only a few species are found in freshwater habitats like *Ranunculus* sect. *Batrachium* and do exhibit the typical habit of water-buttercups (floating, procumbent, and heterophyllous with dissected leaves). *Ranunculus* sect. *Pseudadonis* is holophyletic in Paun et al. (2005), in Hoffmann et al. (2010), and in the total evidence approach by Hörandl and Emadzade (2012). It comprises alpine terrestrial species of the high mountains of New Zealand and is morphologically distinct from the two former sections, *Ranunculus* sect. *Batrachium* and *Ranunculus* sect. *Hecatonia*, by erect habit, basal rosette leaves, and the long beaks of the achenes (Fisher, 1965). The whole group is hexaploid and relationships among species within the section are highly reticulate (Lockhart et al., 2001). Hybridization and adaptive radiation in various ecological niches in the New Zealand mountain systems have probably shaped the diversity of the group.

The acceptance of a paraphyletic section *Hecatonia* preserves information on the complex evolutionary history, on adaptive character evolution, and on the ecology of three different classes: each section can be characterized by six to seven shared characters, and by a distinct ecology and evolutionary history (see Fig. 2; details in Hörandl & Emadzade, 2012). We regard this approach as more informative than the classification of a single clade (III), which would have no shared morphological characters, no predictive quality, and no other information content other than shared ancestry.

The evolutionary history of the paraphyletic *Ranunculus* sect. *Ranunculastrum* has been shaped by the biogeographical history of the ancient Tethyan area (Fig. 4). Phylogenetic and biogeographical analysis by Emadzade et al. (2011) suggests that the orophytic *Ranunculus* sect. *Oreophili* is probably the most ancient group. *Ranunculus* sect. *Ranunculastrum* has already been recognized by most previous authors as a distinct taxon, variously treated as a section, subgenus, or genus (Tamura, 1995, and literature therein), characterized by tuberous roots and elongated receptacles. Most species are found in the Mediterranean and Irano-Turanian regions, with single species occurring in Macaronesia or the Himalayas (Emadzade et al., 2011). Within this clade, the rhizomatous, tuber-lacking *Ranunculus* sect. *Euromontani* with mostly globose fruiting heads (collective fruits) emerged in the European mountain system, thereby rendering *Ranunculus* sect. *Ranunculastrum* paraphyletic (Fig. 5).

A Neighbor-net analysis of molecular data taken from Emadzade et al. (2011) of these two sections and their closest outgroup, *Ranunculus* sect. *Oreophili* (see Fig. 2), was conducted to gain insight into the evolutionary histories of these species (Fig. 5). The analysis shows a narrowly meshed network, without any bootstrap support for alternative splits. In contrast to clade III, a hypothesis of reticulate relationships is not supported, and related species are mostly allopatric or parapatric. Several genetic clusters corresponding to geographical groups appear from this ancestral backbone, but these clusters are only partly congruent with morphological characters connected to two major ecological shifts: the separation of *Ranunculus* sect. *Oreophili*/*Ranunculus* sect. *Ranunculastrum* probably reflects an ancient geographical bifurcation, while the emergence of the orophytic, summer-wet adapted *Ranunculus* sect. *Euromontani* made the group of species of the lowland to mid-altitude, summer-dry adapted *Ranunculus* sect. *Ranunculastrum* paraphyletic. Again, merging of these three groups into one or two clades would just result in a loss of information on biogeographical history, morphology, and ecology (Figs. 2, 4).

POLYPHYLY

Ranunculus also provides good examples for the discrimination of polyphyly and paraphyly. Most of the traditional morphology-based sections recognized by Tamura (1995) turned out to be polyphyletic, or perhaps better, aphyletic, in our phylogenetic analysis (Hörandl et al., 2005; Paun et al., 2005; Hörandl & Emadzade, 2012). The lack of unique synapomorphies for sections, and the mosaic-like character combinations for clades, very much correspond to the scheme shown in Figure 1C. Clades that seem similar based on one character will seem distant based on others, and there are no strong overall patterns of similarity when all characters are applied together. For this reason, although different authors have recognized many of the same subgroups in *Ranunculus*, they have often postulated significantly different relationships among them, resulting in significantly different delineations of the genera in Ranunculeae. This result demonstrates the weakness of purely phenetic approaches for classification in groups that lack unique synapomorphies for the main internal clades. The most obvious example might be the former section *Echinella*, which united several unrelated annual taxa with spines or bristles on the achenes. Presence of spines, bristles, or papillae is highly homoplasious within the genus and can vary even within the same species, but appears mostly in species of dry areas. Life form in *Ranunculus* is variable even within species (Cook, 1966), and the switch to an annual life form happened probably multiple times independently in summer-dry regions with short rainy seasons where a short life cycle is advantageous (Paun et al., 2005; Emadzade et al., 2011).

MONOTYPIC TAXA

Recognizing a single species as a taxon poses the logical problem that a single entity (species) is not a "set," and the same entity must be classified at different levels of the hierarchy (Gregg's paradox; e.g., Buck & Hull, 1966). Many proponents of cladistic classification have regarded monotypic taxa as unacceptable. Evolutionary classification, however, can take a more relaxed approach to the problem as the criterion is not inclusiveness but the amount of modification. Retrospectively, we can trace this change as degree of divergence from the sister taxon. Through their phylograms, Emadzade et al. (2010, 2011) show that genera related to *Ranunculus* display a high degree of divergence, and recognize nine monotypic genera within Ranunculeae (2010). In the phylogram of the total evidence approach in Hörandl

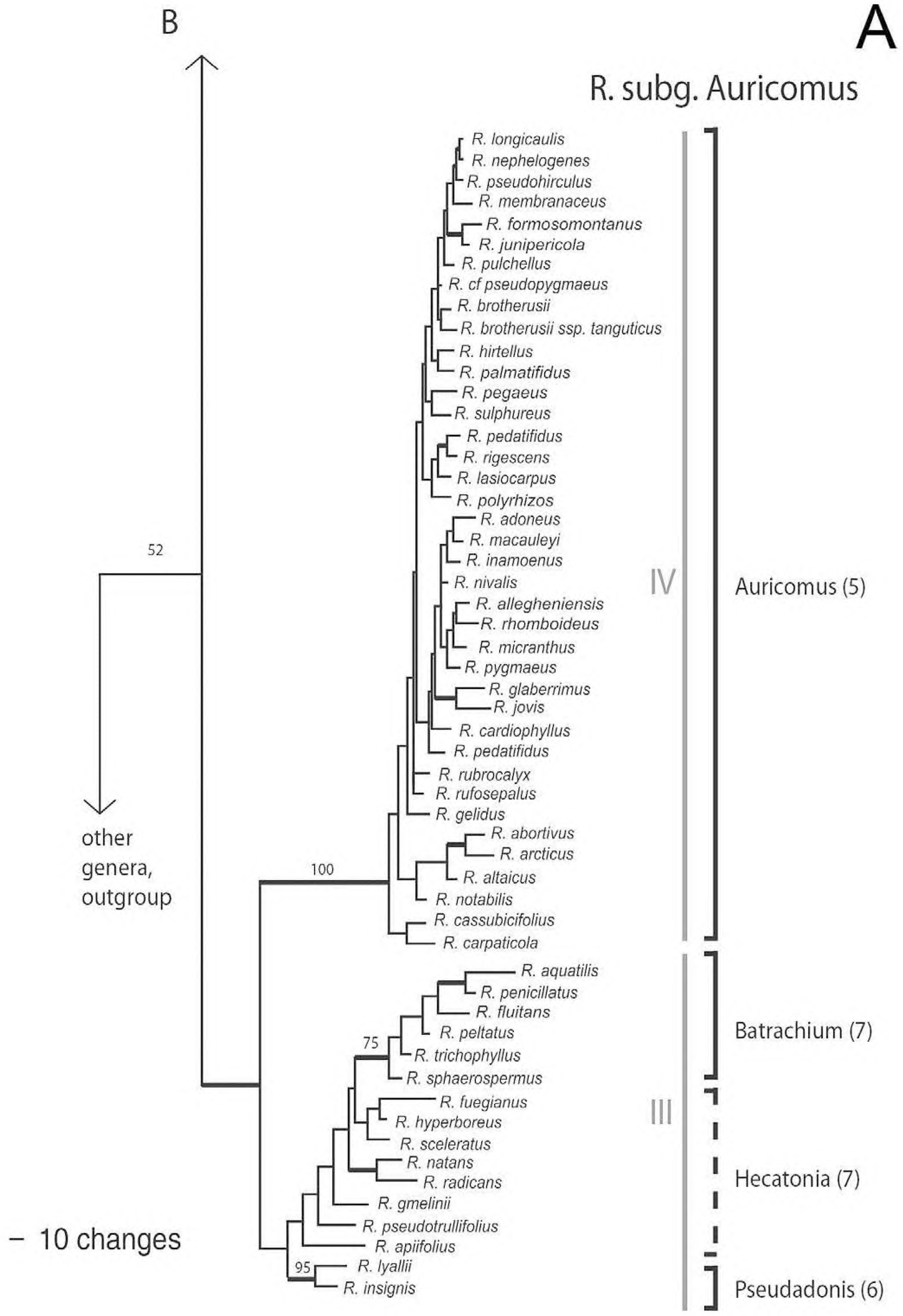

Figure 2. Phylogram of the total evidence analysis (MP) of the combined molecular (sequences of ITS of nrDNA, *matk*, *trnk*, and psbj-petA), morphological (44 characters) and karyological (2 characters) datasets based on 226 samples (outgroup taxa and other genera not shown; tree reprinted from Hörandl & Emadzade, 2012, with modifications). Branches with bootstrap values over 50% are in boldface (for clades representing a section, the bootstrap values are given above the branches). —A. Basal part of the tree belonging to paraphyletic *Ranunculus* subg. *Auricomus*. —B. Upper part of the clade representing *Ranunculus* subg.

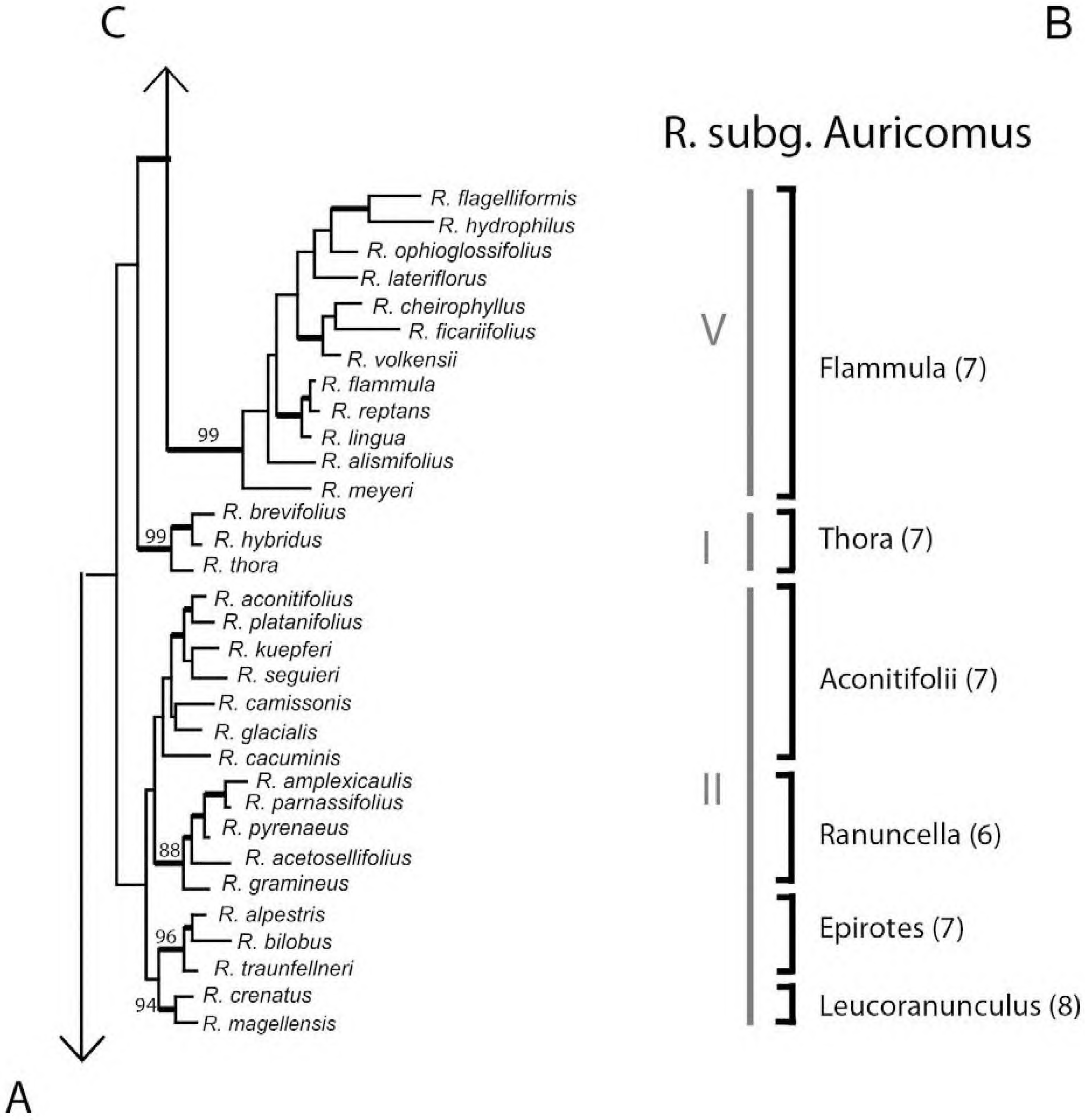

Figure 2. Continued.

and Emadzade (2012), it is clearly evident from branch lengths that divergence among genera is much higher than that among species of *Ranunculus* (Fig. 2). Alternative phylogenetic analyses based on a less complete sampling of genera of the tribe have rendered *Ranunculus* as polyphyletic (Hoot et al., 2008); the authors discussed the possibility of merging all genera of the tribe but did not draw any final formal conclusion. Such a lumping concept does not provide solutions as any taxon is nested in another and emerges out of it; finally *Ranunculus* might end up in a genus including all angiosperms (the "bony fish syndrome"; Brummitt, 2006). Cladistic classification is solely based on branching patterns and does not provide any information on divergence inside clades. Evolutionary classification, in contrast, regards synapomorphies and autapomorphies as crucial criteria for the delimitation of genera (see Stuessy et al., 2014). Interestingly, a high degree of morphological and genetic divergence occurs among genera of Ranunculeae in combination with long-distance dispersal (Emadzade & Hörandl, 2011), which also applies to endemic genera of oceanic islands (see Stuessy et al., 2013). Within *Ranunculus* s. str., such divergence patterns of island endemics are uncommon, at least for morphological divergence. Sections are usually not characterized by acquisition of unique morphological characters along

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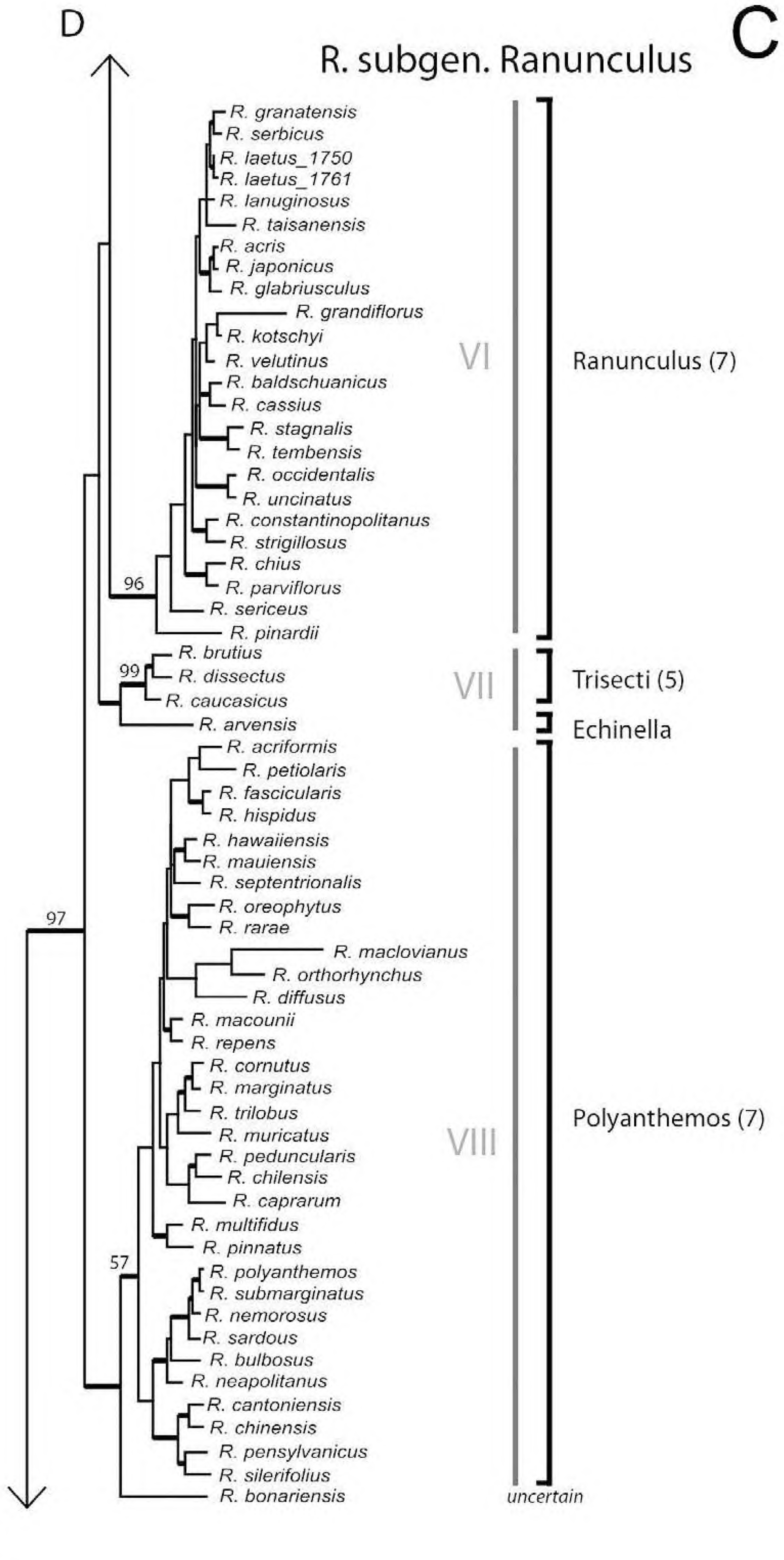
←

Auricomus. —C. Lower part of the clade representing *Ranunculus* subg. *Ranunculus*. —D. Upper part of the clade representing *Ranunculus* subg. *Ranunculus*. Dashed brackets, paraphyletic sections; solid brackets, holophyletic sections, with names of sections indicated on the right. The numbers in brackets next to section names indicate the number of shared morphological and karyological characters for that section. Gray bars with Roman numerals refer to clade numbers of the molecular tree only (see details in Hörandl & Emadzade, 2012). Scale bar indicates number of changes.



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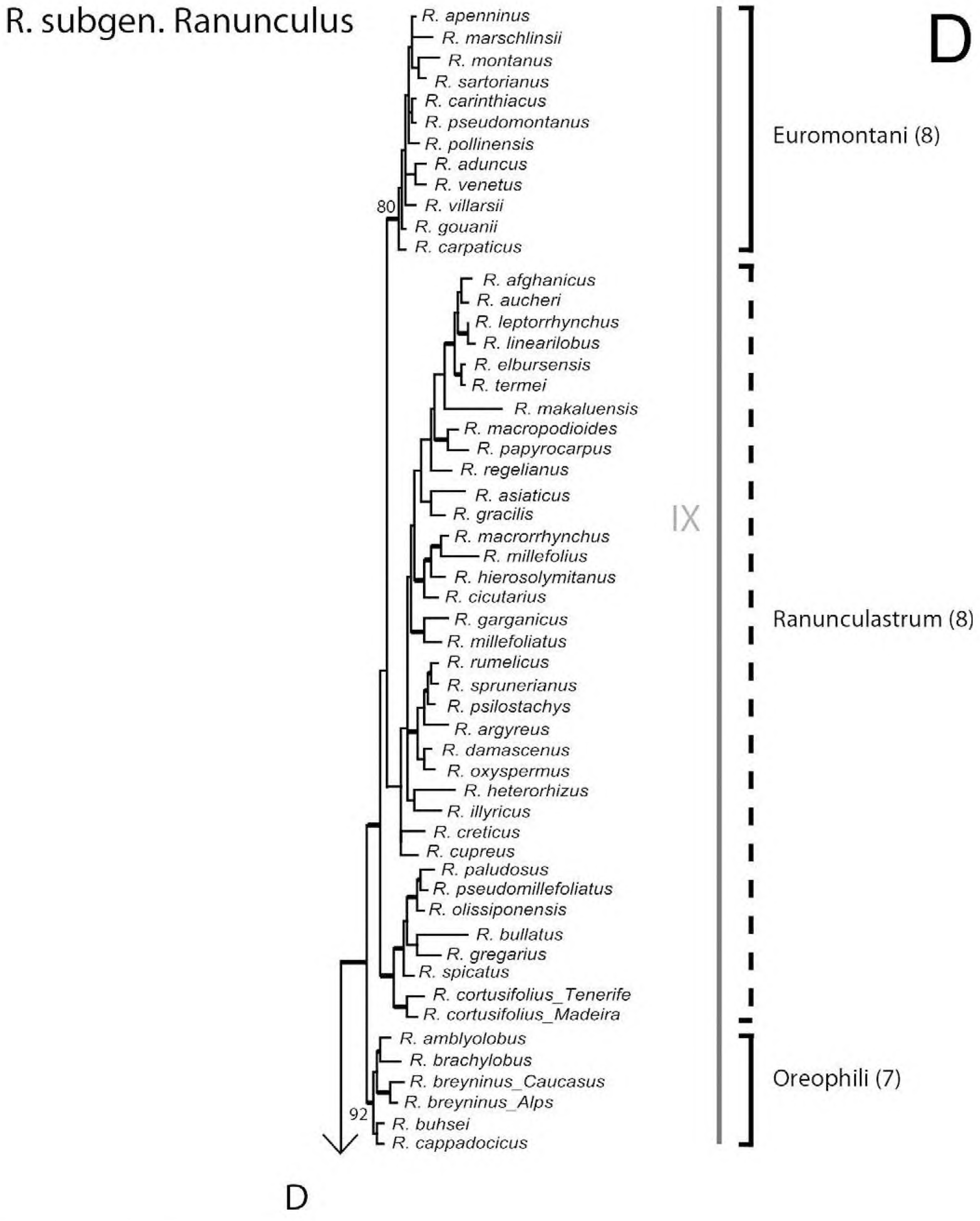

Figure 2. Continued.

a branch; instead, they seem to move between a few common character states, producing a mosaic-like pattern of similarities (Hörandl & Emadzade, 2012).

Ranunculus arvensis is a species with a unique combination of character states: it is an annual with very large, flat achene bodies that are covered with long, sharp spines, a fine papillose microstructure of achene surfaces (Emadzade et al., 2010), and large pollen grains with tricolpate to pantoporate aperture types (Santisuk, 1979). The species is placed on a basal branch of a morphologically heterogeneous clade of species from the Caucasus area and the Irano-Turanian region (VII). Interestingly, *R. arvensis* has a unique, tetraploid karyotype within the genus, consisting of 32 chromosomes of extremely unequal size, and composed of four haploid sets of 4-2-2 or 5-

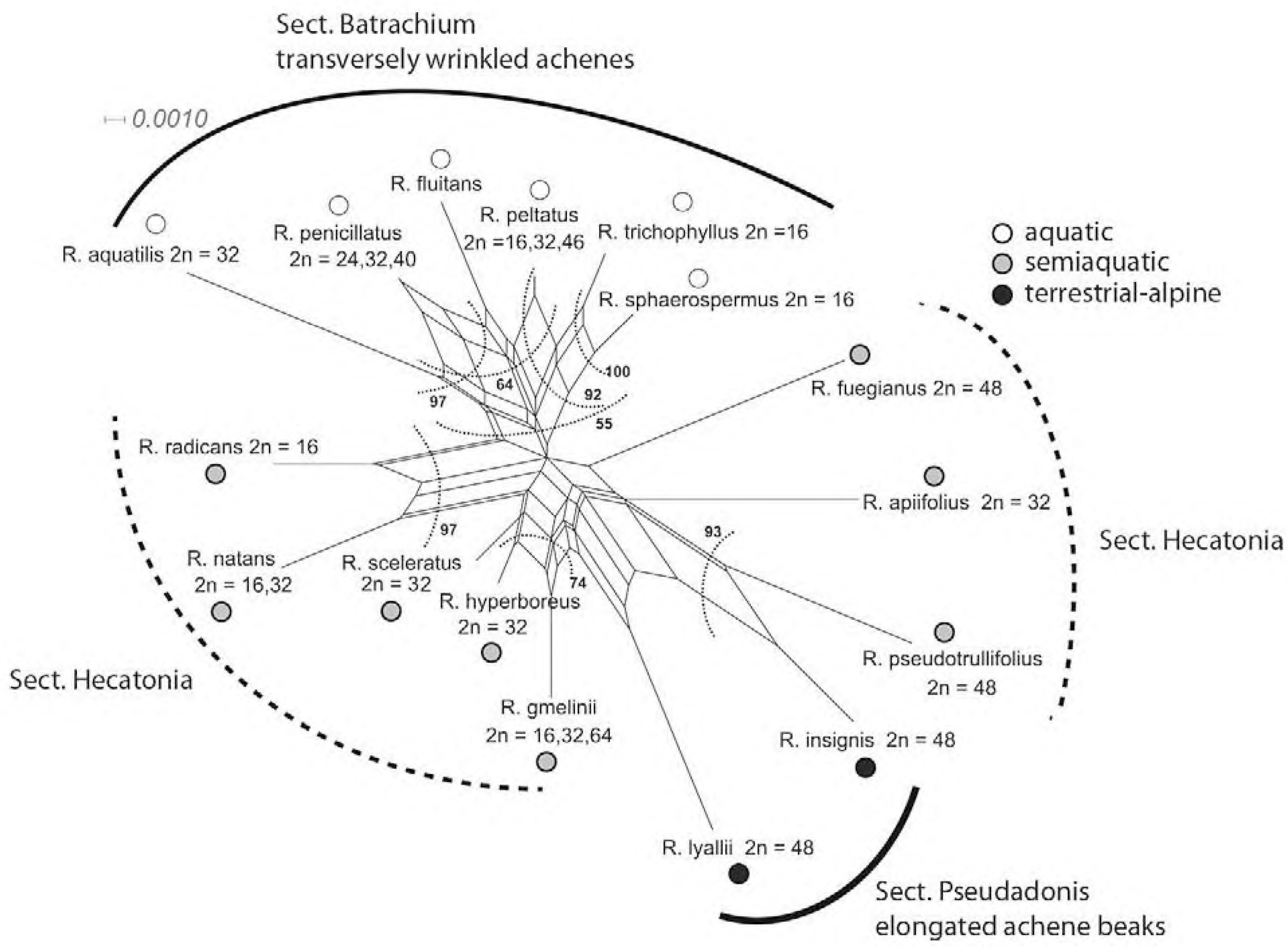

Figure 3. Neighbor-net analysis of clade III based on the molecular dataset only (see Fig. 2; redrawn from Hörandl & Emadzade, 2012), with habitat and karyological information added. Bootstrap values > 50% are shown for main clusters. Scale bar indicates number of changes.

1-2 (acrocentric-submetacentric-metacentric) chromosomes, respectively. The species is probably an allotetraploid of rather unique derivation (Goepfert, 1974). Unfortunately, cytogenetic data are not available for its closest relatives (*Ranunculus* sect. *Trisecti*) and are also not complete enough for phylogenetic analysis. However, a unique karyotype has also been a major criterion for recognizing monotypic taxa in other genera (Stuessy, 2009: 167). Altogether the classification of *R. arvensis* must be regarded as provisional as the information on its sister group is limited, but the present evidence points at a quite isolated position of *R. arvensis* within *Ranunculus*. Our treatment confirms the view of Davis (1960) who proposed that *R. arvensis* should be best treated as a monotypic section.

The information content of a monotypic taxon is mostly that of pronounced divergence (see also Stuessy & König, 2008; Stuessy et al., 2013). It is less relevant whether this divergence is due to an extinction of sister species, leading to a monotypic genus that is relictual, or whether the taxon itself has undergone rapid divergence or even saltational speciation, which may happen in allopolyploids. In both cases, monotypic taxa bear information on evolutionary change, which justifies this type of classification despite some logical inconsistencies.

DISCUSSION

Our classification of *Ranunculus* follows a pluralistic principle: we weigh shared ancestry, genetic and phenotypic similarity, divergence, as well as ecological features, on a case-by-case basis. The varying emphasis on different biological criteria and the lower priority of purely logical criteria (inclusiveness) may be a major point of criticism. However, inclusiveness is meaningless if not connected to biological information.

What kind of information is wanted? Information on descent and shared ancestry is certainly meaningful for understanding evolution, but it is necessarily hypothetical. Moreover, information on descent is in most cases based on a single level of organismic organization, i.e., that of DNA sequences, only; the epigenetic, karyological, and genomic levels are usually not regarded (oddly enough, most authors do not deal with ploidy level variation, although this includes whole genome duplications with all its consequences!). Hence, the biological information content of a clade postulated from sequences of one or two loci remains low, and in tree topologies offers various options for classifying different clades. Clades alone, as groups of descendants, are not yet biological classes, and "cladification" is not yet a classification (Mayr & Bock, 2002). Accepting paraphyletic taxa

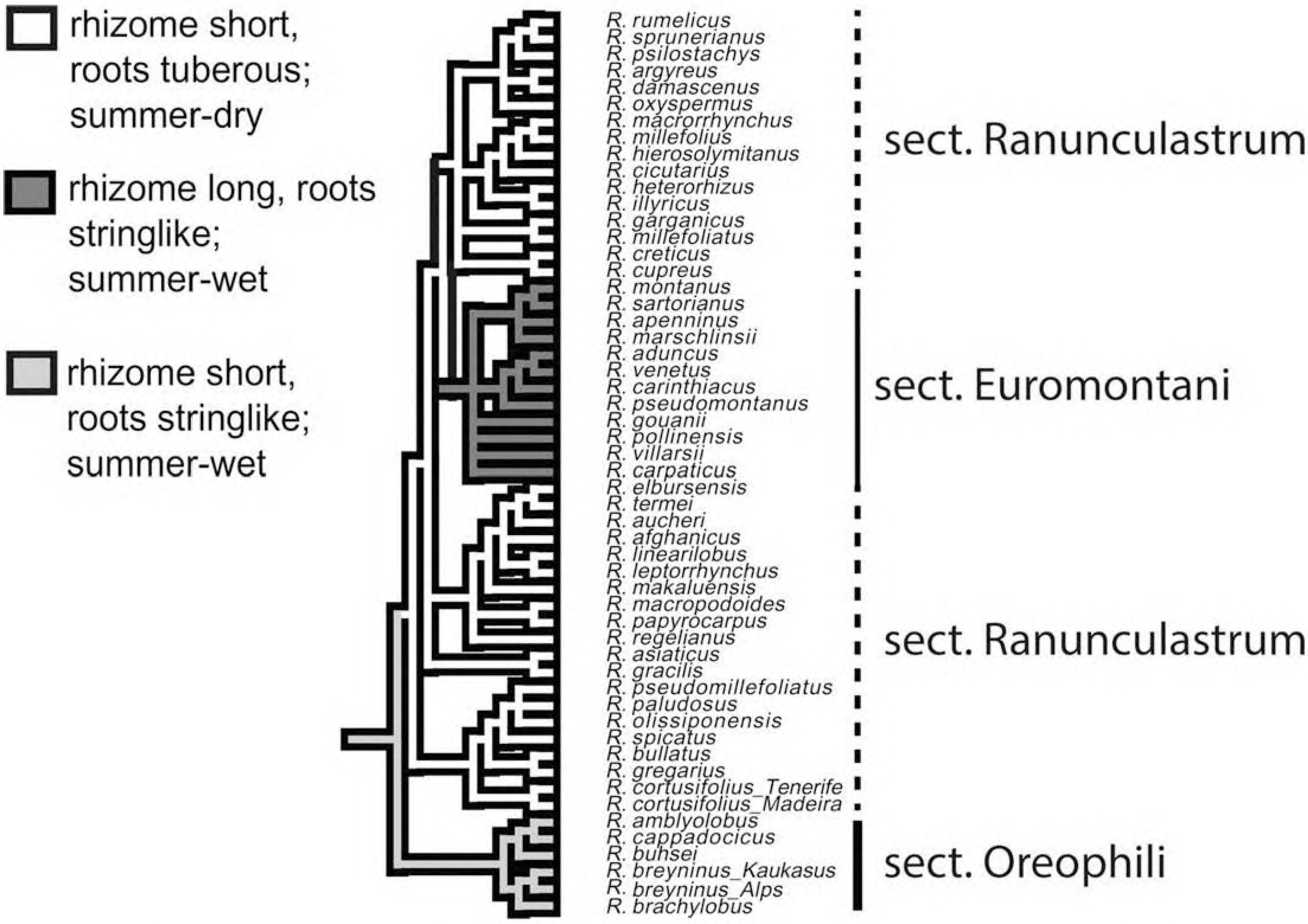

Figure 4. MacClade reconstruction (Maddison & Maddison, 2000) of underground parts mapped onto the molecular tree, clade IX (see Fig. 2D; all data from Hörandl & Emadzade, 2012).

means increasing evolutionary information content at the expense of logical consistency. We do not regard it as justified to subordinate all other levels of information on organisms—from molecular, karyological, genomic, morphological to ecological—under the principle of a strictly logical ordering system, as demanded by cladistics. On the other hand, it is also not desirable to build classifications only around identifiable phenotypes, especially in view of systems biology attempting to integrate genomics, transcriptomics, proteomics, metabolomics, and so forth. All these levels of organismic organizations are a product of descent and shaped by evolution. Phenotypic similarity alone, without regard to descent, gives classifications that may only be informative for the characters that they are based on, and it may allow taxa defined by homoplasious characters, therefore not based on true homology.

This case study has also shown the limitations of classifications that are only based on DNA sequences of a few loci. This can be as uninformative as pure phenetics based on similarity in a few morphological characters. Combining all datasets provides taxa that are based on descent but circumscribed to emphasize overall divergence of morphological and cytological characteristics. Despite the methodological limitations of total evidence approaches, the analysis of combined datasets appears to be powerful to maximize information content. This approach was also useful on higher taxonomic levels in basal eudicots, i.e., for Ranunculales (Wang et al., 2009), where previous descriptive analyses failed to resolve relationships and resulted in different classifications. The taxonomic framework for *Ranunculus* is, of course, still not perfect; it is likely that unresolved branches or weakly supported clades will get better support with the addition of more DNA markers and cytological data. Within the bigger sections, applications of next generation sequencing to collect whole genome or transcriptome data might greatly improve information content for resolving the internal phylogenies of complex sections (e.g., Harrison & Kidner, 2011). The understanding of modification could be greatly improved as well by additional anatomical, embryological, phytochemical, palynological, and other studies, and also by more detailed ecological data. Evolutionary classification will provide a useful framework for such detailed studies as it provides basic information on the modifications of the phenotype.

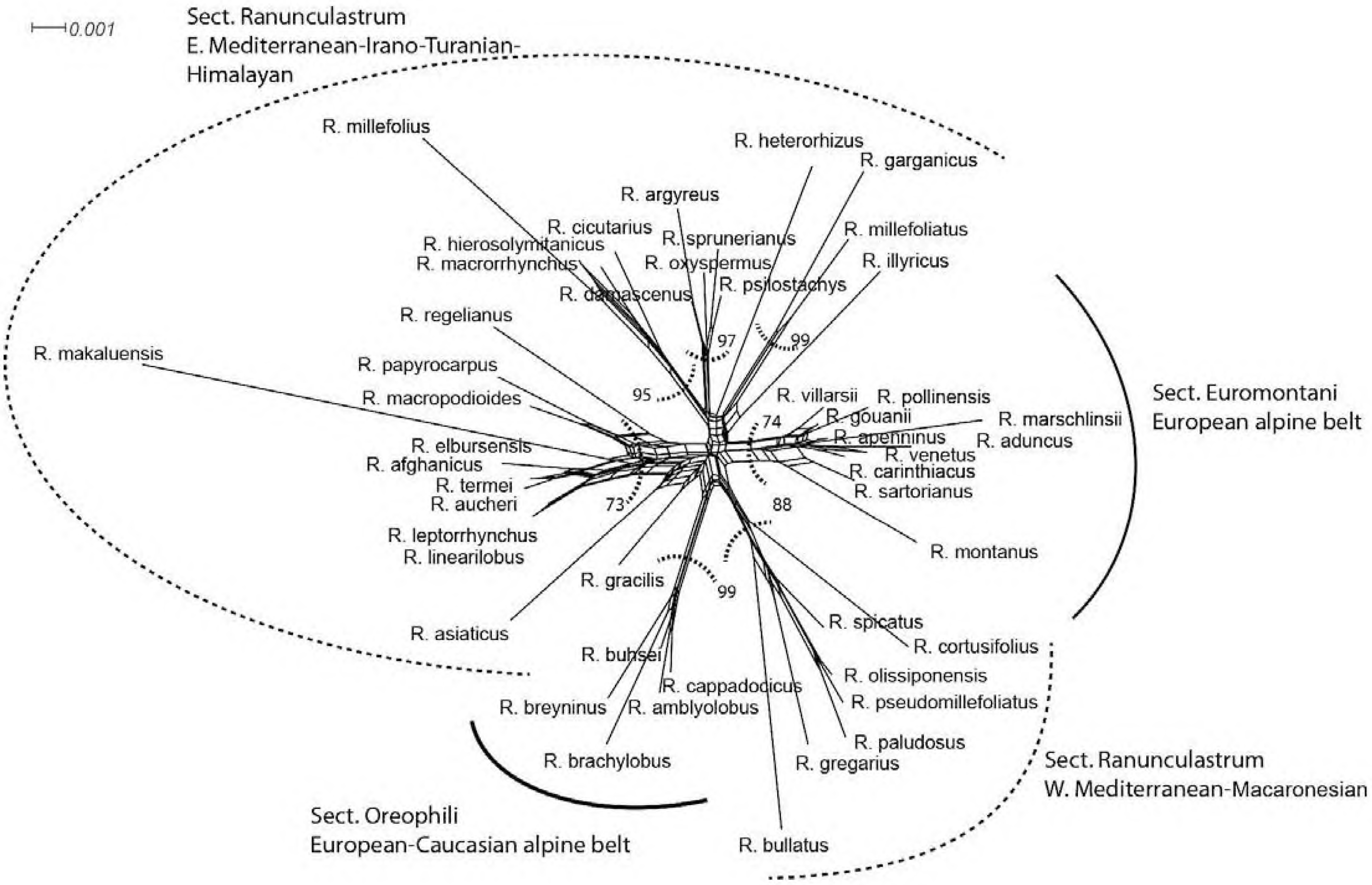

Figure 5. Neighbor-net analysis of clade IX based on the combined molecular dataset (data from Emadzade et al., 2011), using SplitsTree vers. 4.0 (Huson & Bryant, 2006), based on uncorrected p-distances; clusters tested with 1000 bootstrap replicates (values $\geq 50\%$ are shown for main clusters). Scale bar indicates number of changes.

Finally, I would like to address the aspect of information content and practicability. Although many authors rank practicability as the least important criterion (Mishler, 2009), it is an essential feature of information systems to be practicable. For the work of the taxonomist, in fact, the broadening of criteria and datasets effectively reduces the number of equally valid groupings (Fig. 1D). Cladistic classification usually offers many alternative possibilities of selecting groups with shared ancestry (e.g., three in the case of Fig. 1B). Descent alone is a major aspect of evolution, but not a powerful discriminating factor for the definition of biological classes. Phenetics, in contrast, suffers from the many different combinations of character states that produce equally valid patterns of similarity (e.g., four in the case of Fig. 1C). Therefore, phenetics has led to various taxonomic opinions and synonyms, which burdened taxonomy in pre-phylogenetic times. Evolutionary classification has the potential to reduce the number of equally valid groupings: for example, in Figure 1D, only two grouping concepts would be consistent with a criterion of combining phylogeny *and* phenetic similarity: (A, B) and (C, D) or A, B (C, D). In practice, this decision can be based on the degree of divergence case by case. The combination A (B, C, D) and a solution of having four monotypic taxa A, B, C, D are both rejected by phenetic similarities and holophyly of C, D.

We have followed the Linnaean hierarchy for our classification, which of course is artificial, but still widely accepted because of the practicability of ranked hierarchies (Stevens, 2006). The question of appropriate ranking, and the consequence of name changes at different ranks, is not directly resolved by evolutionary classification. In fact, paraphyly could be accepted at different taxonomic ranks: one might follow in *Ranunculus* a concept to classify *Batrachium* or *Ranunculastrum* as genera, rendering the rest of *Ranunculus* paraphyletic. In fact, *Ranunculus* sect. *Batrachium* is the only section that has a unique synapomorphy within the genus. For genera of Ranunculeae, the presence of syn- or automorphies was regarded as an important criterion (Emadzade et al., 2010). However, we considered evolutionary divergence to decide upon the appropriate rank. We did not conduct a patrocladistic analysis (Stuessy & König, 2008); however, the branch lengths of the phylogram of *Ranunculus* and related genera already show that divergence of *Batrachium* from its relatives is lower than divergence among genera (Fig. 2). For this reason, we regard it as more appropriate to keep these paraphyletic groups on the sectional level rather than the generic level.

Evolutionary classification will finally meet the needs of users. In my opinion, taxonomy should not dogmatically override the needs of users, but rather aim at classifications that maximize information for them. In this respect, evolutionary classification can also try to keep the link to traditional classifications and to older literature, where considerable information on phenotype, biogeography, and ecology is being stored. For instance, the name "*Batrachium*" is widely used at various ranks (genus, subgenus, section) in floras and monographs (see surveys in Hörandl et al., 2005; Emadzade et al., 2010). Because of its distinctive features, the circumscription of the taxon has been quite stable in the literature. For the term *Batrachium*, ISI Web of Science lists 56 papers; a Google Scholar search finds 2950 results, and a Google search finds 54,600 results (accessed in April 2012). It would weaken our information systems considerably if we were to sink this taxon into clade III, simply because clade III as a whole has a well-supported hypothesis of a common ancestor. Clade III has never been recognized in this circumscription in the literature, and it is not a class with information content. *Ranunculus* sect. *Hecatonia* does have information content of shared features (see Fig. 2), which differentiates the group from *Ranunculus* sect. *Batrachium*. In this respect, the paraphyletic section *Hecatonia* preserves a well-defined class. Merging sections *Hecatonia* and *Batrachium* would result in a quite heterogeneous group, which would be ecologically and morphologically distinct from *Ranunculus* sect. *Pseudadonis*, but would lose many morphological characteristics. In contrast, *Ranunculus* sect. *Batrachium* is definitely a class, i.e., an information unit; however, this class can be preserved only by breaking with strict inclusiveness and accepting a paraphyletic *Ranunculus* sect. *Hecatonia*, thus recognizing the evolutionary process within the clade. It is necessary to understand how previous literature and modern information systems are linked to worldwide data collection and databasing to document biodiversity, to understand community ecology, species invasions, and extinctions, and to develop conservation strategies. It is further needed for agriculture, forestry, and plant breeding, where traditional literature is still widely used (e.g., Brickell et al., 2008). Modern biology requires more information on taxa than a hypothesis of descent.

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